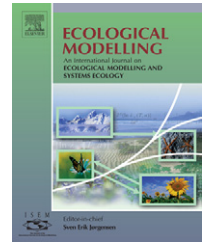


available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/ecolmodel](http://www.elsevier.com/locate/ecolmodel)

# A multi-model framework for simulating wildlife population response to land-use and climate change

Brad H. McRae<sup>a,\*</sup>, Nathan H. Schumaker<sup>b</sup>, Robert B. McKane<sup>b</sup>, Richard T. Busing<sup>c</sup>, Allen M. Solomon<sup>d</sup>, Connie A. Burdick<sup>b</sup>

<sup>a</sup> The Nature Conservancy, 1917 1st Avenue, Seattle, WA 98101, USA

<sup>b</sup> US Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, 200 SW 35th Street, Corvallis, OR 97333, USA

<sup>c</sup> US Geological Survey, 200 SW 35th Street, Corvallis, OR 97333, USA

<sup>d</sup> US Forest Service, RPC4, 1601 North Kent Street, Arlington, VA 22209, USA

## ARTICLE INFO

### Article history:

Received 23 June 2007

Received in revised form

30 July 2008

Accepted 13 August 2008

Published on line 26 September 2008

### Keywords:

Climate change

Land-use change

Alternative future landscape

Habitat change

Population dynamics

Spatially-explicit population model

## ABSTRACT

Reliable assessments of how human activities will affect wildlife populations are essential for making scientifically defensible resource management decisions. A principle challenge of predicting effects of proposed management, development, or conservation actions is the need to incorporate multiple biotic and abiotic factors, including land-use and climate change, that interact to affect wildlife habitat and populations through time. Here we demonstrate how models of land-use, climate change, and other dynamic factors can be integrated into a coherent framework for predicting wildlife population trends. Our framework starts with land-use and climate change models developed for a region of interest. Vegetation changes through time under alternative future scenarios are predicted using an individual-based plant community model. These predictions are combined with spatially explicit animal habitat models to map changes in the distribution and quality of wildlife habitat expected under the various scenarios. Animal population responses to habitat changes and other factors are then projected using a flexible, individual-based animal population model.

As an example application, we simulated animal population trends under three future land-use scenarios and four climate change scenarios in the Cascade Range of western Oregon. We chose two birds with contrasting habitat preferences for our simulations: winter wrens (*Troglodytes troglodytes*), which are most abundant in mature conifer forests, and song sparrows (*Melospiza melodia*), which prefer more open, shrubby habitats. We used climate and land-use predictions from previously published studies, as well as previously published predictions of vegetation responses using FORCLIM, an individual-based forest dynamics simulator. Vegetation predictions were integrated with other factors in PATCH, a spatially explicit, individual-based animal population simulator. Through incorporating effects of landscape history and limited dispersal, our framework predicted population changes that typically exceeded those expected based on changes in mean habitat suitability alone. Although land-use had greater impacts on habitat quality than did climate change in our simulations, we found that small changes in vital rates resulting from climate change or other stressors can have large consequences for population trajectories. The ability to integrate bottom-up demographic processes like these with top-down constraints

\* Corresponding author. Tel.: +1 206 343 4345; fax: +1 206 343 5608.

E-mail address: [bmcrae@tnc.org](mailto:bmcrae@tnc.org) (B.H. McRae).

0304-3800/\$ – see front matter © 2008 Elsevier B.V. All rights reserved.

doi:10.1016/j.ecolmodel.2008.08.001

imposed by climate and land-use in a dynamic modeling environment is a key advantage of our approach. The resulting framework should allow researchers to synthesize existing empirical evidence, and to explore complex interactions that are difficult or impossible to capture through piecemeal modeling approaches.

© 2008 Elsevier B.V. All rights reserved.

## 1. Introduction

Predicting how animal populations will respond to landscape change, climate change, and other anthropogenic and non-anthropogenic stressors is critical to making effective environmental management and conservation decisions. Animal populations are increasingly exposed to multiple natural and anthropogenic threats including habitat loss and fragmentation, direct exploitation, chemical stressors (pesticides, fertilizers, and pollutants), and exotic invasions. A growing concern among wildlife managers and conservationists is that climate change may exacerbate current threats to wildlife through a suite of mechanisms, including (but not limited to) range shifts, habitat loss, changes in food resources, phenological changes, or changes in ecological communities and species interactions (e.g., Crick and Sparks, 1999; Hughes, 2000; McCarty, 2001; Root and Schneider, 2002; Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Travis, 2003). These impacts, when coupled with non-climate threats, may increase the vulnerability of at-risk animal populations and will certainly complicate efforts to forecast their responses to proposed resource development or conservation activities. Indeed, predicting how wildlife populations might respond to future environmental changes against a backdrop of changing climate is one of the major contemporary challenges in conservation biology (Hill et al., 1999; Warren et al., 2001; Norris et al., 2004).

Yet assessments of threats or benefits from management actions are typically driven by a single management question, and they rarely address cumulative or interactive effects of climate and other factors that will affect species of concern. Thus, making scientifically defensible environmental management and conservation planning decisions will require the development of modeling strategies that track how multiple biotic and abiotic factors interact to affect animal populations through time, both through habitat modifications and through other mechanisms. Part of this challenge involves translating impacts on ecosystem processes resulting from land-use and climate change into temporal trends in wildlife habitat. Doing so requires the linkage of mechanistic models of climate, land-use, vegetation, and demographic responses of animal populations to habitat characteristics (Holt et al., 1995). Because habitat pattern is a key driver of wildlife population dynamics (Gilpin, 1987; Dunning et al., 1995; Turner et al., 1995; Hansen et al., 1999; Wiegand et al., 1999), such modeling frameworks must explicitly consider the influence of spatial heterogeneity on population performance (Cairns, 1993; Johnson, 2002; Schumaker et al., 2004; Topping and Odderskær, 2004). Additionally, because changes in mean habitat suitability often correlate poorly with population performance (Lawler and Schumaker, 2004; Schumaker et al., 2004), assessments should project actual population sizes of

species of concern. Finally, whereas most efforts to predict population responses to land-use or climate change have involved simulating populations in static landscapes representing some future condition (e.g., Schumaker et al., 2004; Jepsen et al., 2005), a more accurate representation of the complex, non-linear responses of populations will require dynamic landscape simulations that track the interaction of habitat changes and non-habitat-mediated factors through time (Dunning et al., 1995; Holt et al., 1995; Root and Schneider, 2002).

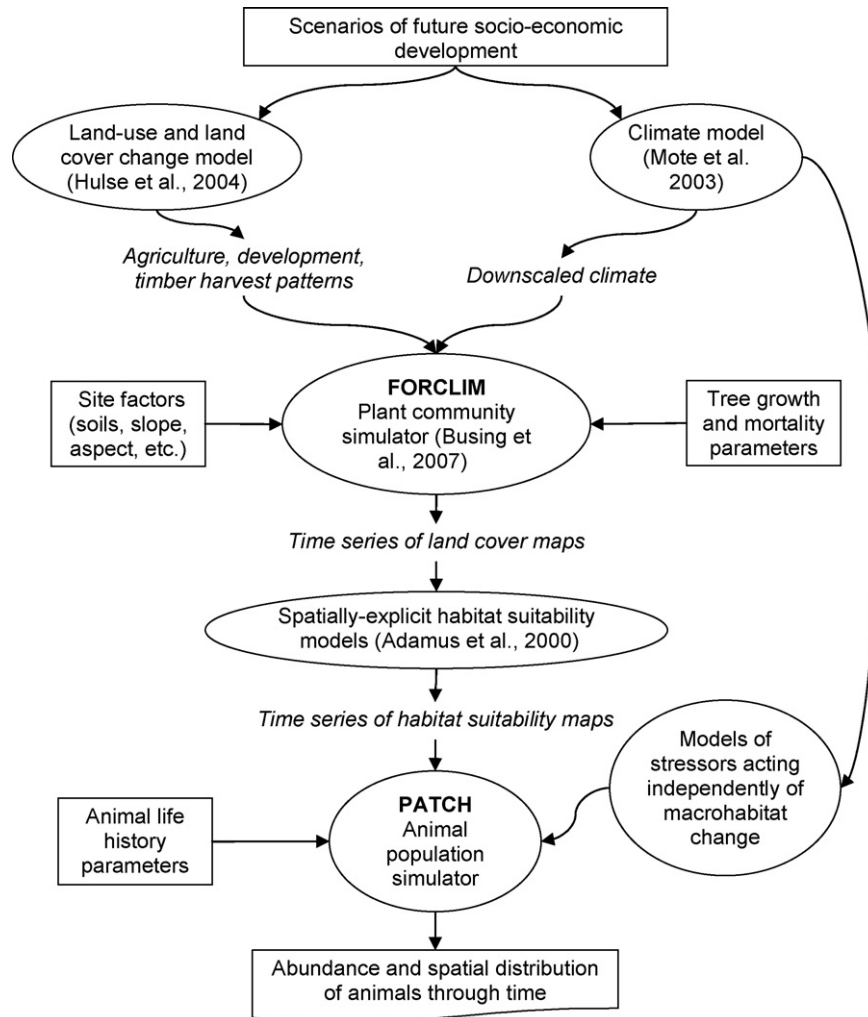
Here we illustrate how recent advances in individual-based plant and animal population models can help achieve these goals. The first objective of this study was to develop a modeling framework for simulating dynamic spatial and temporal changes in habitat and animal populations in response to climate change, land-use and other stressors occurring within complex landscapes. The framework is spatially explicit, incorporates mechanisms that act either via habitat modifications or directly on various aspects of species' life histories, and is not landscape-, species-, or threat-specific.

Our second objective was to apply the framework to a 500 km<sup>2</sup> forested watershed in the western Oregon Cascades to illustrate its use for projecting and analyzing long-term (1990–2060) population trends for two bird species having contrasting habitat requirements. We modeled population trajectories of winter wrens (*Troglodytes troglodytes*) and song sparrows (*Melospiza melodia*) as they responded to three future land-use scenarios and four climate change scenarios. The resulting simulations illustrate a flexible modeling approach incorporating effects of diverse factors interacting within a real landscape and producing spatially explicit projections of changes in habitat quality and wildlife populations through time. We demonstrate how the framework improves upon previous approaches, discuss its limitations, and suggest potential improvements.

## 2. Methods

### 2.1. Model framework

Our modeling framework (Fig. 1) combines top-down constraints (climate and land-use) and bottom-up processes (e.g., tree growth and competition, individual birth, death, and dispersal events of animals) to model trends in animal habitat and population dynamics through time. First, predictions from climate models are downscaled to predict future climate patterns in the region of interest under various future climate scenarios. These are integrated with predictions of future land management actions under alternative development scenarios using an individual-based tree growth model. The model produces a time series of maps of vegetation structure and composition, which are then converted into maps of



**Fig. 1 – Modeling framework.** The framework could be expanded to include other inputs (such as additional anthropogenic stressors) or other submodels (such as ecohydrology models to predict changes in soil moisture or intermittent streams and wetlands as inputs to FORCLIM and wildlife habitat models).

animal habitat suitability using spatially-explicit habitat models.

Habitat maps are integrated with other factors driving animal populations using an enhanced version of the PATCH animal population simulator (Schumaker, 1998). The flexibility of PATCH allows incorporation of not only of factors that affect populations via habitat modifications, but also those that act directly on the survival, fecundity, or dispersal behavior of individuals at different life stages, in different habitats, or at different time steps. Importantly, model inputs and outputs are all spatially explicit. Our example application uses climate, land-use, vegetation, and wildlife habitat models assembled from previously published studies; these models are summarized below. Animal population simulations implemented specifically for this study are described in greater detail.

## 2.2. Study area

We illustrate how these disparate models can be combined into an informative framework by applying them to animal populations in the Upper South Santiam Watershed (USSW),

located within the Willamette National Forest on the western slope of the Oregon Cascade mountain range. Elevations in the 500 km<sup>2</sup> watershed range from 200 to 1780 m above sea level. The watershed spans three major vegetation zones, characterized by late-successional tree species ranging from Western hemlock (*Tsuga heterophylla*) at lower elevations, to Pacific silver fir (*Abies amabilis*) at moderate elevations, to mountain hemlock (*Tsuga mertensiana*) at higher elevations. Douglas-fir (*Pseudotsuga menziesii*) currently dominates early-, mid- and late-successional stands throughout most of the watershed, with increasing abundance of species such as Pacific silver fir and mountain hemlock at higher elevations.

The complex topography and forest cover of the watershed provide habitat for a broad array of wildlife populations. The major factor driving changes in these populations during the past century has been habitat alteration associated with forest management. Harvest of forest products, fire suppression, road construction, and other management activities have altered essentially every part of the landscape, creating a mosaic of vegetation types that is historically unique. While forest management will remain an important factor during

the next century, projected climate changes are expected to become increasingly significant (Mote et al., 2003).

### 2.3. Wildlife species

We chose two animal species according to the following criteria. First, we wanted to simulate population sizes of species expected to respond differently to habitat change, and we therefore sought species with contrasting habitat requirements. We also required that the species be year-round residents of the study area (to avoid confounding effects of changes in survival on wintering grounds), that their occurrence in the study area would be unlikely to be affected by range shifts, and that demographic data be available for both. Because demographic data are generally more available for birds than for other animal taxa, we focused our search for candidate species on songbirds.

Winter wrens (*T. troglodytes*) and song sparrows (*M. melodia*) fit the above criteria well. Both species are exceptionally well-studied, with demographic data on Pacific Northwest populations available from several sources. The species also have highly complementary habitat needs; winter wrens are most abundant in mature forests, whereas song sparrows occupy primarily early successional habitats, including clearcuts. Habitat suitability index (HSI) models have been developed for both species by an expert panel (Adamus et al., 2000), and the models were assigned the highest possible confidence ratings by the panel. Finally, because they both have broad latitudinal and elevational distributions (Arcese et al., 2002; Hejl et al., 2002), the ranges of these species appear less likely to shift out of the study area in response to climate change than other candidate species.

### 2.4. Land-use and climate scenarios

Our land-use scenarios included three “alternative future” scenarios, described in detail by Hulse et al. (2002, 2004), reflecting potential changes in urban and rural development, agriculture, and forestry practices for the period 1990–2050. For the USSW, the “Plan Trend 2050” scenario projects changes in land cover expected through 2050 if existing forest management plans are implemented as written and current trends continue. The “Conservation 2050” scenario depicts consequences of shifts in forest management toward habitat preservation and restoration, for example, the establishment of old-growth reserves. In contrast, the “Development 2050” scenario reflects shifts toward more intensive harvest policies emphasizing forest products. Impacts of the different

land-use scenarios on vegetation in the USSW were predicted by Busing et al. (2007) using the FORCLIM forest dynamics simulator (Bugmann, 1996; Busing and Solomon, 2004, 2005, 2006). The simulations of Busing et al. (2007) were tailored to produce maps that would be interpretable as wildlife habitat for this study.

In addition to changes in land-use, our simulations also incorporated the effects of four climate change scenarios (Table 1). The first scenario reflected current climate conditions, whereas the second and third reflected lower and upper extremes projected by a set of global climate models (Mote et al., 2003): minor warming with drier summers, and major warming with wetter conditions. Under the minor climate change scenario, temperature was increased by 0.5 °C in 2025 and by 1.5 °C in 2045. Winter precipitation (October to March) was increased 2% in 2025 and decreased 2% in 2045, whereas summer precipitation (April to September) was decreased 4% in 2025 and 7% in 2045. For the second scenario, temperature was increased by 2.6 °C in 2025 and by 3.2 °C in 2045. Winter precipitation was increased 18% in 2025 and 22% in 2045, and summer precipitation was increased 14% in 2025 and 9% in 2045. As with the land-use scenarios, these climate scenarios affected wildlife populations through habitat changes simulated by FORCLIM only.

Our fourth climate scenario illustrates how mechanisms acting independently of macrohabitat change may be incorporated into population predictions. Even with minor climate change, for example, drier conditions during the breeding season could limit food resources, phenological changes could result in timing mismatches between brood rearing and peaks in insect population cycles, populations of exotics (including predators or competitors) could increase, or disease and parasite dynamics could change (McCarty, 2001; Root and Schneider, 2002; Parmesan and Yohe, 2003). As such, this scenario incorporated habitat effects due to the minor climate change scenario described above, but also assumed that additional mechanisms would affect populations independently of macrohabitat change predicted by FORCLIM. Because hypotheses of how climate change may directly affect these two species have not yet been proposed, we did not attempt to forecast the effects of any particular stressor mechanism. Instead, our objective was to explore how one of many plausible scenarios could be incorporated into our modeling framework. We considered a conservative scenario in which minor climate change caused a small (5%) reduction in fecundity across all habitats that took effect gradually (over 50 years) as the climate warmed.

**Table 1 – Four climate scenarios considered in vegetation and animal population simulations**

Climate scenario	Climate conditions (Mote et al., 2003)	Habitat-independent climate change effects
(I) No climate change	Current climate	None
(II) Minor climate change, habitat effects only	Minor warming with drier summers	None
(III) Major climate change, habitat effects only	Major warming with wetter conditions	None
(IV) Minor climate change with demographic effects	Minor warming with drier summers	5% fecundity decline phased in over period 2000–2040



## 2.5. Vegetation response to land-use and climate change

We incorporated potential effects of future land-use and climate change scenarios on vegetation using the predictions of Busing et al. (2007) for the USSW. Busing et al. simulated vegetation response to climate change and land-use across the landscape using FORCLIM, an individual-based forest dynamics simulator designed to predict responses in forest composition and structure to climatic change in space and time (Bugmann, 1996). The model is based on tree-level responses to precipitation and temperature regimes, and predicts stand development and succession as a tree-by-tree growth and replacement process. For each species, key parameters include maximum diameter at breast height, height, and age, as well as a set of functions describing growth response to resource availability and a set of conditions for ingrowth. Busing and Solomon (2004, 2005, 2006) tested FORCLIM extensively across a wide range of climatic zones and ecoregions in western Oregon, demonstrating that the model can be used to predict the complex patterns of forest biomass, productivity and plant community composition in this region. Busing and Solomon (2006) also enhanced FORCLIM to include fire disturbance, with larger trees of fire tolerant species exhibiting the greatest survivorship. For their USSW study, Busing et al. (2007) simulated fire regimes to match those inferred from historical fire data.

To establish climate change scenarios for FORCLIM, Busing et al. (2007) first identified ten climate zones within the USSW based on daily, high-resolution (50-m cell size) maps of temperature and precipitation. Daly et al. (2007) developed these data by modifying the PRISM climate model to include orographic effects for spatially interpolating data from nine weather stations within and adjacent to the USSW. Busing et al. (2007) then constructed zone-specific climate scenarios by linearly interpolating inter-annual trends that started with baseline climate in 1990 and passed through temperature and precipitation values projected by Mote et al. (2003) for 2025 and 2045. Similarly, land-use (harvest) scenarios were constructed based on stand ages projected by Hulse et al. (2002, 2004) for the year 2050. The 2050 stand ages were used to infer date of last harvest, and forest stands younger than 60 years in 2050 were harvested at the appropriate time steps during FORCLIM simulations. FORCLIM output passed to habitat suitability sub-models in our framework consisted of stand age and basal area by tree species at 30-m pixel sizes, with updates made at 10-year intervals.

**Table 2 – Habitat suitability scores from Adamus et al. (2000)**

Landscape class	Winter wren	Song sparrow
Conifer 0–20 years	2	7
Conifer closed 21–40 years	4	1
Conifer closed 41–60 years	6	1
Conifer closed 61–80 years	8	1
Conifer closed 81–200 years	9	2
Conifer closed 200+ years	10	2
Mixed forest closed	8	2
Hardwood closed	2	1
Conifer semiclosed upland	7	2
Mixed forest semiclosed upland	5	3
Hardwood semiclosed upland	2	4
Tree open upland	0	7
Shrub dry, tree open, semiclosed, valley	0	9
Christmas trees	0	5
Grass tall	0	1
Built low density	0	7

Only habitat types with nonzero scores for at least one species are shown.

## 2.6. Habitat models and demographic parameters

Following simulations of future land cover patterns, the next step in our framework (Fig. 1) was to convert land cover maps into maps of habitat suitability using spatially explicit habitat suitability models. We applied models developed by Adamus et al. (2000), who used four expert panels to define species–habitat relationships for winter wrens, song sparrows, and 277 other bird, mammal, amphibian, and reptile species throughout the 28,000 km<sup>2</sup> Willamette River Basin, of which the USSW is part. The panels rated each species' use of 34 habitat types occurring throughout the basin, with each habitat type assigned an HSI rating from 0 to 10 representing the species' relative preference for breeding in the habitat type (Table 2). The ratings were then modified using adjacency rules that took into account effects of nearby habitat features on focal pixels, described in detail in Adamus et al. (2000). For winter wrens, the adjacency rules increased suitability of habitat adjacent to wetlands and riparian areas. For song sparrows, the rules increased suitability of habitat adjacent to wetlands, shrub classes, and in edges between wooded and open cover types.

**Table 3 – Demographic parameters used for PATCH simulations**

Species	Territory size (ha)	Movement distance (km)	Fecundity	Survival	1990 population size	
					Nominal	Simulated
Winter wren	0.7	5	1.85	0.375	2308	2295 (35)
Song sparrow	0.21	1	1.53	0.470	283	294 (8.5)

Territory size represents the area actively defended during the breeding season, while fecundity is defined as the number of female offspring per female per year to survive to fledgling stage. Nominal population sizes reflect extrapolations from three Breeding Bird Survey routes, while simulated population sizes reflect average 1990 simulated population sizes over 240 replicates, with average 20-replicate standard errors for the 12 scenarios shown in parentheses.

Demographic rates used to parameterize the PATCH model for each species were taken from several empirical studies, and are listed in Table 3. Survivorship rates for both species were based on MAPS (Monitoring Avian Productivity and Survivorship; DeSante et al., 1993) data from the Pacific Northwest. Other demographic parameters for winter wrens were based on field data reported by Armstrong (1955), McLachlin (1983), Cramp (1988), Carey et al. (1991), and Hejl et al. (2002). Parameters for song sparrows were derived from data reported in Nice (1937), Halliburton and Mewaldt (1976), Sogge and van Riper (1988), Arcese (1989), Arcese et al. (1992, 2002), and Smith et al. (1996). We estimated baseline (1990) population sizes using data from three North American Breeding Bird Survey (BBS; Peterjohn and Sauer, 1993) routes within and adjacent to the USSW. We averaged the maximum count from the routes for the most recent 5 years for which data were available, and calculated densities assuming a detection distance of 200 m for both species (Rosenberg, Cornell Lab of Ornithology, personal communication, 2005). Present-day population sizes were estimated by multiplying these densities by the area of the watershed.

## 2.7. Animal population model

PATCH (program to assist in tracking critical habitat; Schumaker, 1998) is a spatially explicit, individual-based, animal population simulator. PATCH is currently a females-only model that incorporates demographic stochasticity through the use of a pseudorandom number generator to evaluate the outcome of each individual survival and reproduction event. It reads raster GIS maps of habitat and stressor distributions, and converts these maps into arrays of hexagonal cells. For simplicity, we set the hexagon size equal to the mean territory size for a female of each species (Table 3). PATCH stores survival and reproduction rates as Leslie matrices (Leslie, 1945), but it links these values to habitat quality or stressor intensity, which are in turn stored as hexagon-specific attributes. The actual survival and fecundity rates experienced by an individual therefore vary depending on the spatial attributes associated with the territories they occupy.

Our PATCH life cycles begin with any landscape change that is scheduled for the year. This is followed by the optional movement of adults and then juveniles, which provides individuals an opportunity to respond to the landscape change, relocate from a poor site, or fledge. Survival and breeding decisions are made next, and the year ends with a census event. Individuals will preferentially disperse to hexagons with higher scores within the limits of the maximum dispersal distance for the species (Table 3). We assumed that fecundity and survival rates experienced by individual birds increased linearly from zero (hexagon without any habitat) to the values shown in Table 3 (hexagon composed entirely of the best habitat). Further description of the PATCH model can be found in Schumaker (1998) and Schumaker et al. (2004).

## 2.8. Animal population response to land-use and climate change

We performed PATCH simulations for each of the twelve combinations of land-use and climate change scenarios to

investigate their relative impacts on the two bird populations. We constructed a time series of hexagon maps for each species, with hexagon scores corresponding to mean habitat suitability scores at each time step. To characterize demographic stochasticity, 20 replicates were run for each scenario for a total of 240 replicate runs for each species. Simulations spanned the 110-year time period from 1990 to 2100 (following a 200-year “spin-up” with the 1990 landscape in order to minimize effects of initial conditions and to allow populations to stabilize). Following spin-up, we tracked performance of both populations from 1990 forward, with hexagon scores changing at 10-year intervals from the years 2000 to 2050 to reflect landscape trends predicted by FORCLIM (Busing et al., 2007). For the climate scenario in which fecundity changed over time, we used habitat maps from the minor climate change scenario, but decremented fecundity rates by 1% per decade from 2000 to 2040. Fecundity rates were held constant at 95% of their nominal values for the remaining simulation years.

Our primary endpoint for comparison among scenarios was mean population size (taken across multiple replicate simulations) at the year 2060, which allowed the simulated populations 10 years to respond to the final landscape change event. In addition, we continued the simulations through the year 2100 (still using the 2050 landscape) in order to better illustrate the population trajectory present at year 2060 and isolate effects of any lag in population responses to landscape updates.

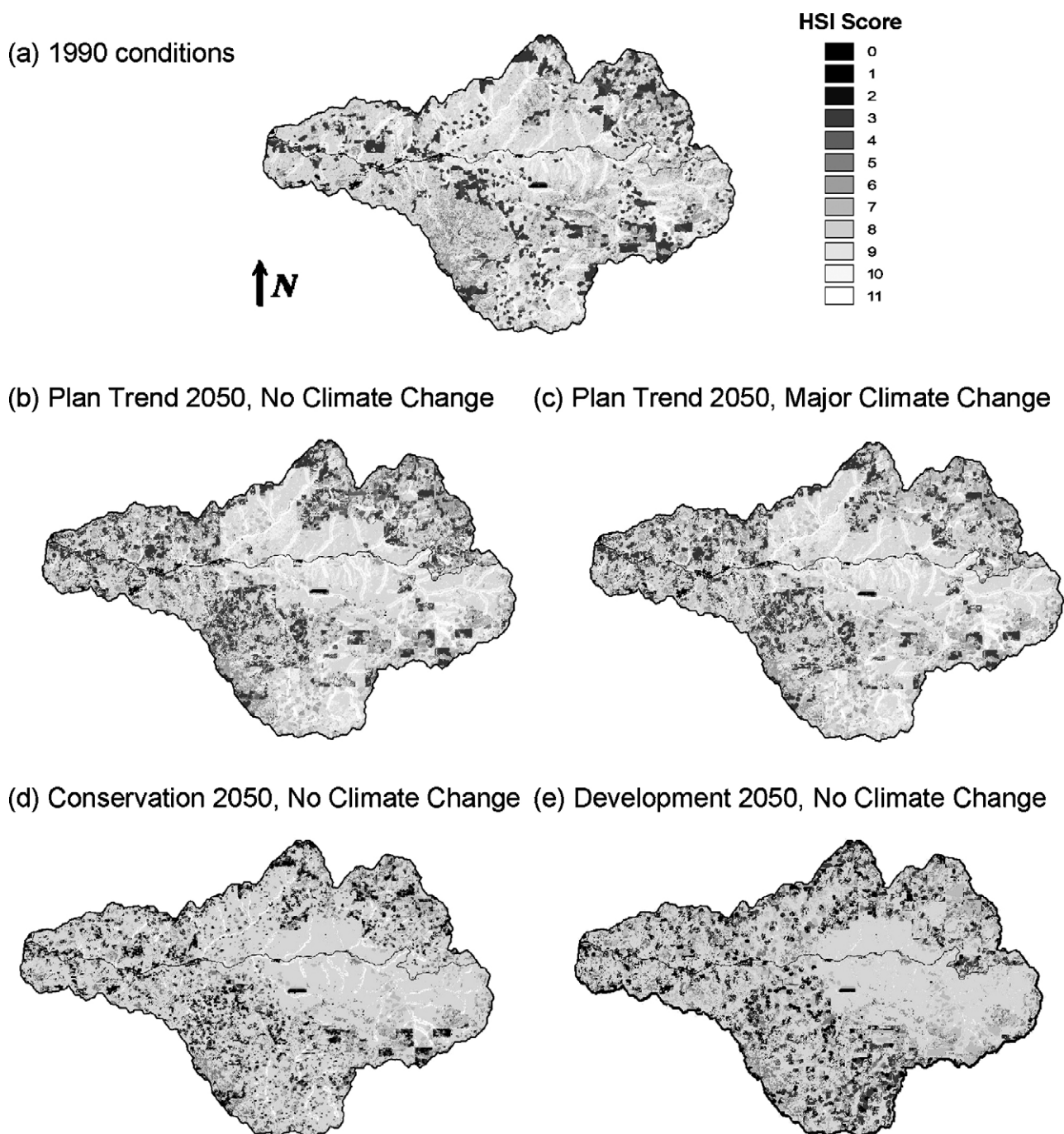
# 3. Results

## 3.1. Changes in wildlife habitat

For winter wrens, mean HSI values based on FORCLIM predictions for 2050 increased a maximum of 4.1% (Conservation scenario, major climate change) and decreased a maximum of 1.9% (Plan Trend, no climate change) relative to 1990 values. Mean HSI values for song sparrows increased a maximum of 3.4% (Plan Trend, major climate change) and decreased a maximum of 11% (Development, no climate change) relative to 1990. Habitat changes (e.g., for selected scenarios shown in Figs. 2 and 3) were primarily driven by conversion of coniferous stands to early seral stages by forest harvest, or conversion to older seral stages through stand growth. In contrast to considerable habitat impacts of different land-use scenarios, climate change had little effect on habitat quality for either species (Figs. 2–4, and 5a and b). Slight improvements in habitat quality resulting from the two climate change scenarios were associated with landscape-level shifts in tree species distributions that converted many early seral stage forest stands from “conifer closed” to “mixed forest closed” land cover types.

## 3.2. Population trends in response to land-use

Land-use had substantial effects on populations of both species throughout the simulation period (Fig. 4). Winter wrens declined initially in all scenarios, but began to recover in the conservation scenario following the 2040 land-



**Fig. 2 – Maps of habitat suitability index (HSI) scores for winter wrens under (a) 1990 conditions. (b) Plan Trend 2050 scenario without climate change. (c) Plan Trend 2050 scenario with major climate change. (d) Conservation 2050 scenario without climate change. (e) Development scenario without climate change. Lighter shades indicate higher quality habitat.**

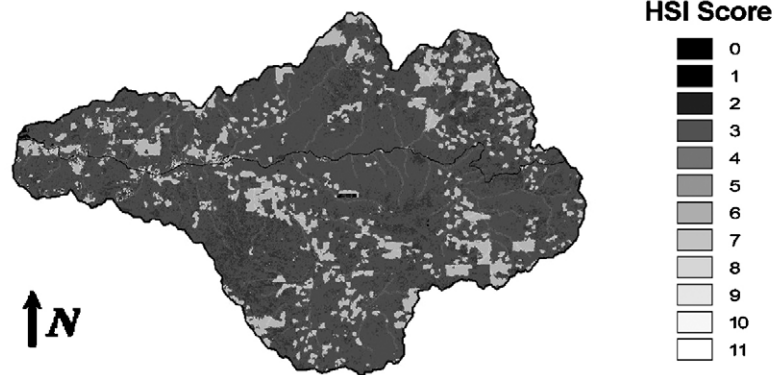
scape update. In contrast, song sparrows showed substantial declines following the 2000 landscape update, with later recoveries in all scenarios.

Populations generally changed more than did mean HSI scores. Fig. 5 shows changes in mean habitat suitability under the twelve land-use and climate change scenario combinations, along with changes in mean population sizes in 2060 and 2100 for each case. The largest population changes

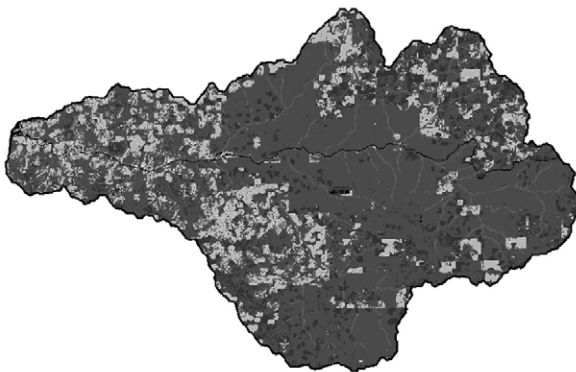
for winter wrens were observed under the development scenario, in which populations declined steadily with numbers in 2060 and 2100 reflecting reductions of 25% and 35%, respectively, relative to 1990 values. For song sparrows, greatest departures from 1990 population sizes were observed under the development scenario, with populations declining by up to 28% before beginning to increase again (Fig. 4).



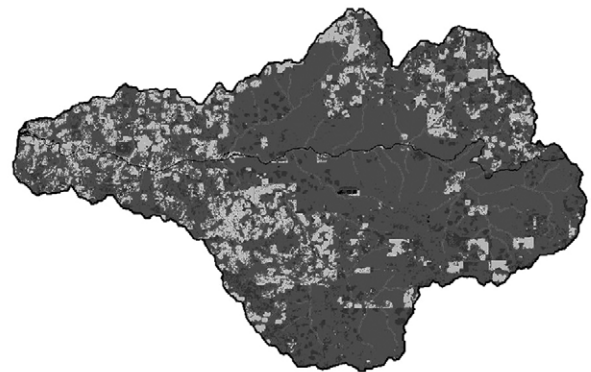
(a) 1990 conditions



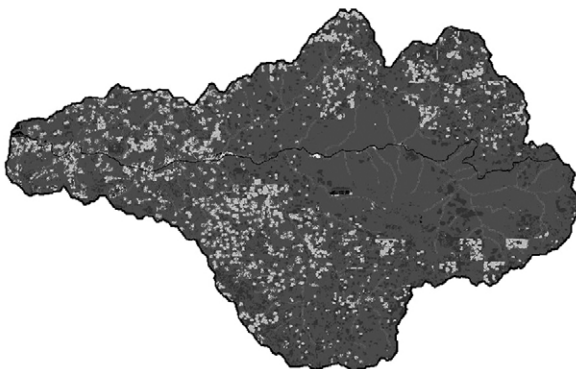
(b) Plan Trend 2050, No Climate Change



(c) Plan Trend 2050, Major Climate Change



(d) Conservation 2050, No Climate Change



(e) Development 2050, No Climate Change



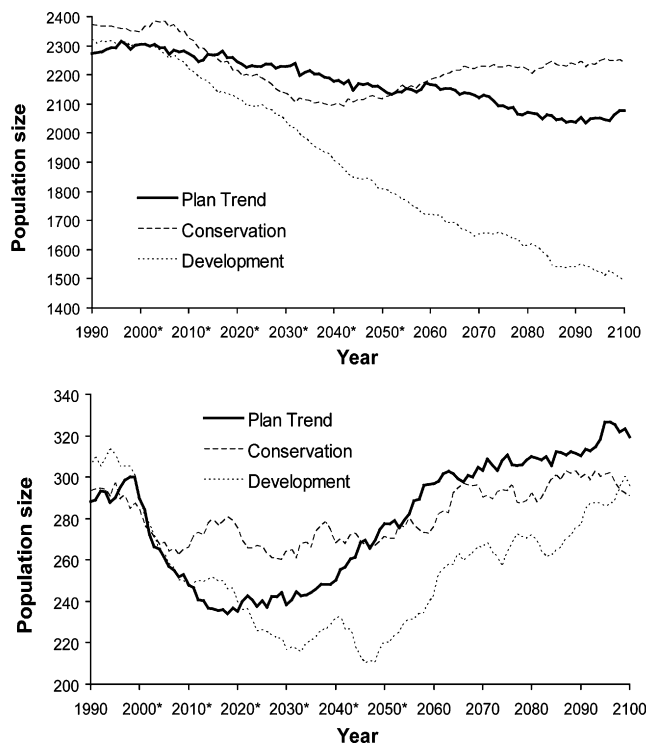
**Fig. 3 – Maps of habitat suitability index (HSI) scores for song sparrows under (a) 1990 conditions. (b) Plan Trend 2050 scenario without climate change. (c) Plan Trend 2050 scenario with major climate change. (d) Conservation 2050 scenario without climate change. (e) Development 2050 scenario without climate change. Lighter shades indicate higher quality habitat.**

### 3.3. Population trends in response to climate change

The two warming scenarios that acted strictly through habitat changes had negligible consequences for the simulated bird populations (Fig. 5c–f), but the scenario in which minor warming gradually reduced fecundity via habitat-independent mechanisms caused large declines in populations across

all land-use scenarios (Fig. 5g–j). With minor warming and reduced fecundity, winter wren populations declined an average of 47% and 61% by 2060 and 2100, respectively, and song sparrows declined an average of 30% and 27%, respectively. For both species, maximum declines resulted from the combination of the reduced fecundity climate scenario and the development scenario, with winter wrens declining by 55%





**Fig. 4 – Population trends through time across the three land-use scenarios, without climate change, for (a) winter wrens and (b) song sparrows. Asterisks indicate years in which landscape updates from FORCLIM were implemented. Differences in 1990 population sizes among the three scenarios are due solely to the stochastic nature of our simulations. Standard errors for mean population sizes in any given year ranged from 20 to 50 for winter wrens and 5.8 to 13 for song sparrows.**

and 71% in 2060 and 2100, respectively, and song sparrows declining by 39% and 32%, respectively (Fig. 5g–j).

### 3.4. Habitat changes as predictors of habitat-driven population trends

Even for the scenarios in which climate and land-use affected populations via habitat changes alone, changes in mean HSI values relative to 1990 were poor predictors of population trends. Across the three land-use scenarios and the three climate scenarios in which populations responded only to habitat changes, correlations between mean 2050 HSI values and 2060 population sizes were particularly weak for winter wrens ( $R^2=0.13$ ,  $P>0.05$  based on Spearman rank correlation test); populations in 2100 better reflected 2050 HSI values, although the relationship was still nonsignificant ( $R^2=0.24$ ,  $P>0.05$ ). Correlations between mean HSI values and population endpoints were stronger for song sparrows ( $R^2=0.37$ ,  $P<0.05$  in 2060;  $R^2=0.78$ ,  $P<0.05$  in 2100). However, because mean HSI values for song sparrows in 2050 clustered at two extremes with no intermediate values among the various scenarios (Fig. 5b), these correlations likely overstate the ability of mean HSI values to predict future song sparrow population trends.

## 4. Discussion

Most attempts to predict changes in plant and animal populations resulting from climate change have employed static models, i.e., those that do not capture the transient sequence of events that would take place as species respond to changing climate (e.g., Carey and Brown, 1994; Erasmus et al., 2002). Only recently have plant or animal simulations incorporated climate conditions that evolve over time (e.g., Dullinger et al., 2004; Tews et al., 2007). The ability to simulate animal habitat and populations as they respond to continuously changing climate and land use is a key feature of our modeling framework; differences between our simulation results under static and dynamic landscape conditions show the importance of incorporating transient effects of ecosystem change, as discussed below.

A second key feature is the synthesis of land-use and climate change predictions using individual-based models. Although previous studies have linked plant or animal population models with dynamic landscape models (e.g., Akcakaya et al., 2004; Larson et al., 2004), and some have incorporated effects of both climate change and land use (e.g., for shrub cover, Tews et al., 2006; for salmon, Battin et al., 2007), we are unaware of any other study that has integrated the effects of both using individual-based plant and animal population models. The use of individual-based approaches at these two crucial modeling steps means that the effects of both top-down and bottom-up processes affecting animal populations can be modeled with considerable mechanistic detail and at fine-grained temporal spatial scales. For example, PATCH allows incorporation not only of mechanisms affecting populations that act via macrohabitat modifications, but also of those that act directly on the survival, fecundity, or dispersal behavior of individuals at different life stages, in different habitats, or at different time steps. This versatility sets the stage for realistic assessments of diverse threats to wildlife populations from multiple natural and anthropogenic stressors that may act synergistically, such as pesticide use, habitat loss, and climate change. It also allows assessment of benefits from management actions such as habitat restoration, connectivity conservation, and reintroduction or translocation of individuals.

Finally, the spatially explicit output of PATCH allows a more robust analysis of model behavior than would be possible with projections of overall population sizes alone. This allows important effects of habitat heterogeneity to be examined in detail, as illustrated below.

### 4.1. Interpretation of simulation results

Our modeling framework establishes a means for integrating the effects of land-use, climate and other stressors on habitat quality and wildlife populations, while enabling analyses of the relative contribution of individual stressors to projected net responses. With regard to impacts on habitat quality, our simulations for 1990–2050 indicate that climate change slightly improved average HSI scores across the USSW for both winter wrens and song sparrows. However, climate-driven habitat changes were small, which is reasonable because 60

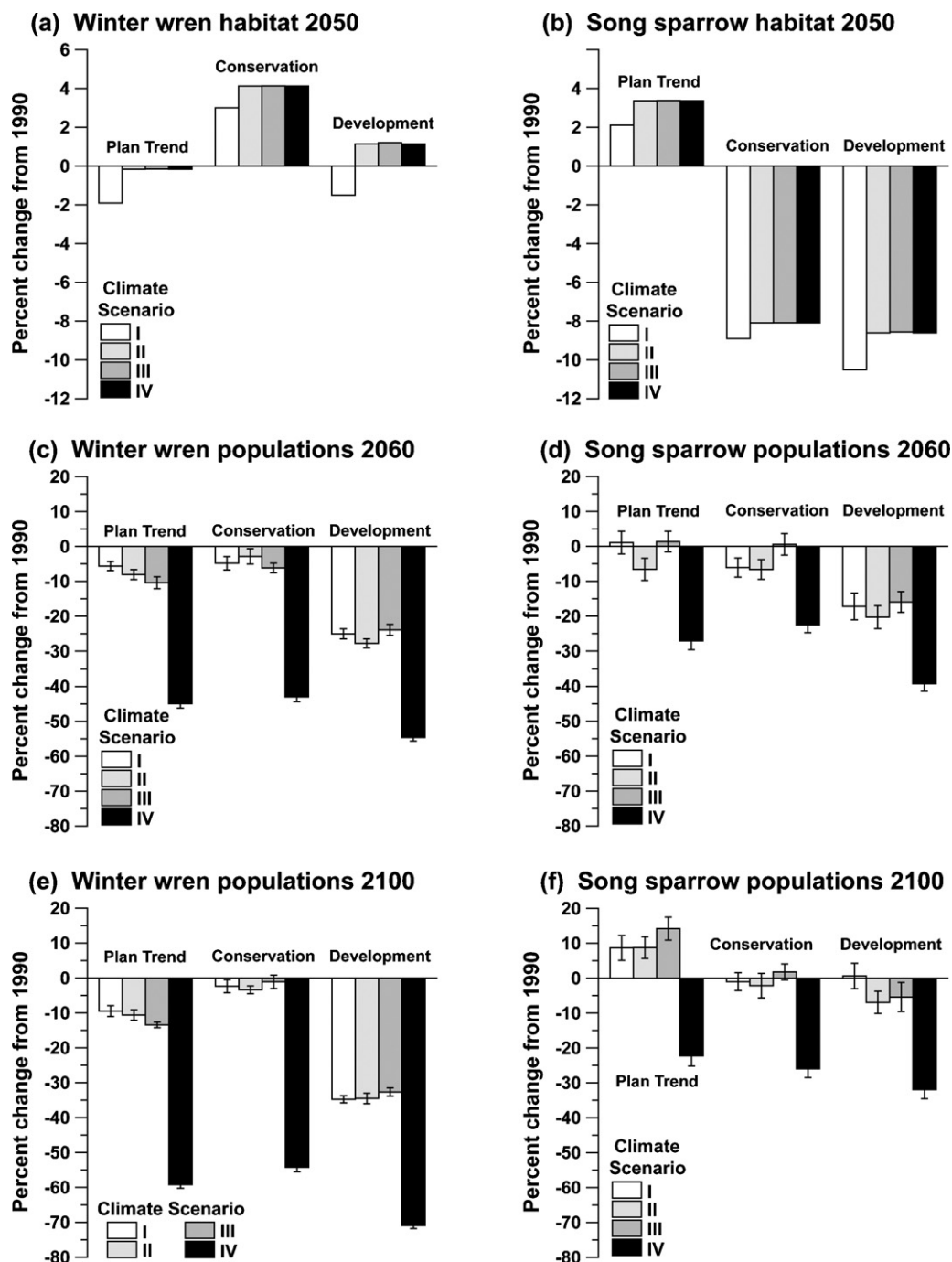


Fig. 5 – Changes in simulated habitat and population sizes for winter wrens and song sparrows relative to 1990 for the 12 land-use and climate change scenario combinations. (a and b) Changes in mean HSI scores. (c and d) 2060 population sizes relative to 1990. (e and f) 2100 population sizes relative to 1990. Climate scenario I: no climate change. Climate scenario II: minor climate change with habitat-only effects. Climate scenario III: major climate change with habitat-only effects. Climate scenario IV: minor climate change with 5% decline in fecundity phased in over the period of 2000–2040. Mean population changes shown with standard error bars.

years is a short time for vegetation structure and composition to respond to altered climate. By contrast, our simulations predicted significant habitat and population differences between the three land-use scenarios.

Even though land-use driven macrohabitat changes exceeded those caused by climate change, our simulations

show how climate-driven mechanisms that act independently of macrohabitat characteristics can have large impacts on animal populations as well. Our fourth climate scenario, in which fecundity was gradually reduced by 5%, was a surrogate for potential impacts of mechanisms acting independently of macrohabitat modifications. The small decline in fecun-

dity we modeled can be considered conservative considering large impacts observed in natural populations (e.g., Sillett et al., 2000). As such, our simulations suggest that even small changes in vital rates resulting from climate change or other stressors could result in population responses that dwarf those caused by the habitat trends we modeled. For example, when combined with the conservation land-use scenario, the fourth climate scenario resulted in winter wren populations that were an average of 41% smaller in 2060 than those in which fecundity remained unchanged; by 2100, the reduced fecundity populations were an average of 53% smaller (Fig. 5). Here, modest improvements in average HSI scores across the landscape did little to offset even small effects on vital rates that could result from climate change or other stressors. Such effects would likely be amplified via interactions with other species (exotics, predators, competitors, prey, parasites) whose vital rates are also changing, making responses to climate change less predictable and potentially much more significant (Davis et al., 1998; Root and Schneider, 2002). Given the considerable uncertainty about mechanisms and the potential for large effects on populations, there is a critical need for future research in this area.

However, even the results of our simulations that considered changes in macrohabitat alone provide general insights relevant to wildlife modeling and management. Several patterns are worth expanding upon. First, in agreement with earlier modeling efforts (e.g., Schumaker et al., 2004), changes in habitat suitability averaged over the landscape were poor predictors even of relative population responses. For example, even though mean habitat suitability increased for winter wrens in all conservation and two out of three development scenarios, populations declined in all six cases. And, although mean HSI values changed more across the study area for song sparrows, winter wren populations experienced greater changes in population sizes relative to 1990 values.

A closer look at the output from our simulations shows that these patterns result from spatial heterogeneity and differential impacts of habitat change among habitat types of different HSI values. For example, an examination of winter wren birth and death rates across the landscape from 2060 to 2100 points to effects of a decline in hexagons with high HSI scores, due to an unequal distribution of habitat changes among hexagons in different HSI classes. That is, changes in scores of high-quality breeding sites had greater effects than changes in scores of low-quality areas. These findings are similar to those of Johnson (2002), in which the addition of toxicants to high-quality habitat patches had greater impacts on simulated populations than the same toxicant addition to lower quality habitat patches. The relative insignificance of increased mean HSI scores under climate change are also likely attributable to this phenomenon.

In another example of spatial heterogeneity effects, we found that song sparrows disappeared from portions of the study area in the development scenario, even though some high-quality hexagons remained in these areas. An examination of spatial patterning of active territories through time revealed that this can be attributed to the limited dispersal distances of song sparrows, which restricted their ability to colonize newly created habitat as it became available. The effects of fragmentation on species' ability to colonize new

habitats are well known (Meffe and Carroll, 1994), and have been documented empirically for other songbirds (e.g., Villard and Taylor, 1994; van Langevelde, 2000). This result illustrates the ability of PATCH to incorporate connectivity effects resulting from the spatial pattern of landscape change by integrating habitat heterogeneity and species dispersal behavior. Schumaker et al. (2004) documented a similar response to habitat fragmentation for several wildlife populations using the same wildlife population model. That study also illustrated how a net decline in mean habitat quality can be correlated with an increase in population size, depending on the spatial patterns of habitat gain and loss.

A second consistent result was that allowing simulations to run to the year 2100 under static (year 2050) landscape conditions improved correlations between HSI and population size by removing transient effects of landscape conditions prior to 2050, and allowing populations to more fully adjust to the capacity of the 2050 landscape. Thus, models simply based on habitat suitability can be expected to closely match predictions based on dynamic simulations only when landscapes are (unrealistically) presumed to be static. Even so, when landscape conditions were held constant from 2050 to 2100, average HSI values remained relatively poor predictors for winter wren populations ( $R^2 = 0.24$ ,  $P > 0.05$ ).

The above factors combined to produce population responses to the three land-use scenarios that were somewhat counterintuitive. For example, winter wren populations in 2060 and 2100 declined slightly under the conservation scenario, even though reduced logging under this scenario could be reasonably expected to improve wren habitat. Indeed, simulated mean wren habitat suitability did increase under this scenario from 1990 to 2050. These surprising results can be explained by considering the spatial arrangement of habitat changes and the time required for forest stands to recover from logging. For winter wrens, much of the change in mean HSI under the conservation scenario resulted from improvement in low to moderate quality wren habitat (for example, stands that had been recently harvested in 1990 entering 21–40 and 41–60 years stand ages). Increases in high-quality wren habitat were only slight, in part because of the limited availability of forest stands in medium age classes in 1990 that could move into later age classes during our simulations. Thus, populations were not able to benefit from policies favoring wren habitat by 2060. Additionally, because available climate and land-use datasets did not allow us to project landscape changes beyond 2050, the 2100 population endpoints likely underestimate performance of wren populations in this scenario. Nevertheless, these simulations emphasize that wildlife species dependent on late successional habitats are likely to respond very slowly to conservation actions.

#### 4.2. Flexibility of modeling framework

Depending on data, scenarios, and hypotheses available, our framework could be expanded at each modeling step to incorporate additional mechanisms affecting populations. For example, hydrological changes, such as changes in soil moisture and intermittent streams and wetlands, will have important consequences both for tree growth and for riparian-associated animal species (such as the two considered here).

Such changes could be incorporated into our framework by adding an ecohydrology submodel which would further modify water and nutrient availability in FORCLIM, as well as availability of riparian habitat for animals. Additionally, animal range shifts in response to altered temperature and precipitation regimes could be considered via additional submodels that combine climatic and environmental variables to predict changes in range extents (e.g., [Berry et al., 2002](#); [Matthews et al., 2004](#)), allowing simulation of how range shifts and land-use may interact to affect population viability ([Travis, 2003](#)). Finally, changes to land-use practices in response to changing climate ([Dale, 1997](#)) could also be considered.

The current framework and models could also be refined without the addition of new submodels. Vegetation and habitat suitability submodels could be modified to provide greater detail, e.g., predictions at finer spatial or temporal scales or of changes in understory composition. Additionally, the vegetation simulations of [Busing et al. \(2007\)](#) considered only monthly means for temperature and precipitation, but simulations at daily time steps could incorporate additional parameters important for vegetation change, such as daily temperature extremes. Moreover, the period of 1990–2050 is a very short time in which to observe changes in forest structure in response to climate change. Longer simulations will be necessary to elicit large-scale habitat changes, especially in regions like the Pacific Northwest where forest succession occurs over centuries or millennia.

Within PATCH, more spatially complex demographic effects of stressors could also be incorporated; for example, rather than decreasing fecundity uniformly across all habitats, stressor impacts may vary from place to place, with vital rates changing in different ways in different habitat types. PATCH allows such mechanisms to be incorporated directly by independently altering survival, fecundity, or dispersal characteristics in different habitats, at different locations, and at different time steps (e.g., to reflect localized pesticide applications or range contractions). The effects of some vegetation types or portions of a landscape becoming ecological traps ([Gates and Gysel, 1978](#)), in which species preferentially disperse to habitats in which they experience negative growth rates, could be incorporated in this way. Additionally, the generality of PATCH has been enhanced by the addition of modules that allow the formation of social groups (e.g., packs and flocks), and the assembly of territories of irregular shape. Future enhancements to PATCH, such as modeling multiple interacting species, will provide additional flexibility in evaluating risks and benefits to animal populations of changing landscapes, stressors, and management actions.

#### 4.3. Model validation and uncertainty

In our framework, predicted population behavior arises from predictions of submodels (including climate, land-use, tree growth, and habitat), and the traits and behaviors of the simulated individuals. For these reasons, efforts to assess the validity of future modeling efforts will need to focus first on parameters and submodels, and later on patterns that emerge from simulated interactions between individuals and their environment ([Grimm and Railsback, 2005](#)). Because our modeling framework and its submodels are meant to

predict events that have yet not occurred, they cannot be validated in the strict sense ([Oreskes et al., 1994](#); [Araújo et al., 2005](#)). Still, models such as these can be assessed by “hindcasting,” i.e., predicting past sequences of events, as has been done with many climate change models (e.g., [Santer et al., 1996](#)). A second assessment strategy is to substitute space for time, i.e., to test models against independent data from new regions, as has been done with FORCLIM ([Busing and Solomon, 2004, 2005](#)), species-habitat models (e.g., [Fielding and Haworth, 1995](#)), and species-climate envelope models (e.g., [Araújo et al., 2005](#); [Randin et al., 2006](#)). Excellent discussions of the limitations of model validation and assessment, and how they bear on purposes appropriate for simulation modeling, are provided by [Oreskes et al. \(1994\)](#), [Araújo et al. \(2005\)](#), and [Grimm and Railsback \(2005\)](#).

Nevertheless, anything approaching true validation of complex modeling frameworks such as ours will be rare because of the cost and difficulty involved. Thus, assessing uncertainty in model predictions will be especially important. Considerable uncertainty exists in both the structure (which mechanisms and variables are included or excluded) and parameters (values assigned to the variables) of linked models such as ours. Moreover, the linkage of numerous models will substantially increase the potential for error propagation ([Conroy et al., 1995](#); [Holt et al., 1995](#); [Ellner et al., 2002](#); [Larson et al., 2004](#)). Although errors in underlying models are not magnified by spatially explicit models ([Mooij and DeAngelis, 1999](#)), gathering the data necessary to parameterize each of these submodels will be difficult, and predictions resulting from these efforts must be interpreted with care ([Ruckelshaus et al., 1997](#)). There will therefore be a need to quantify uncertainty in model parameters, and to determine whether uncertainties in specific parameter values or stressor scenarios have disproportionate impacts on predicted population trends ([Jorgensen, 1986](#); [Dunning et al., 1995](#)). An important aspect of our framework is that it will allow evaluation of the impacts of uncertainty as it propagates through different submodels.

#### 4.4. Conclusions and future prospects

We did not set out to predict actual future population sizes, but to demonstrate how disparate factors affecting populations can be integrated into a system of linked simulation models. As a result, the suite of ecological mechanisms we considered was limited, and we wish to emphasize that our results should not be taken as absolute forecasts for the coming decades. Still, the general trends predicted under different assumptions about land-use and climate change provide useful insight for future management and research efforts. We found that for the species, study area, time period, and limited mechanisms we considered, our models point to larger macrohabitat changes from land-use than from climate change. Yet this result is tempered by our additional finding that consequences of more direct (and less predictable) impacts of climate change on species' demographic rates may be much larger still. Given the considerable uncertainty about such impacts, a priority should be placed on evaluating and developing models and field data that will improve



our understanding of the processes through which climate change may directly affect species' life histories.

When the goal is to assess relative consequences of alternative management actions for wildlife populations against a background of changing climate and land-use, we see few alternatives to using coupled, spatial simulation models to track habitat, stressor, and population changes through time. The need for careful model construction, parameterization, and evaluation will mean that such undertakings will be costly. Even when resources and data are plentiful, simplifications will be necessary to make modeling efforts tractable, and the precision of predictions will always be limited (Dunning et al., 1995). Still, our results support previous assertions (Bart, 1995; Conroy et al., 1995) that such modeling efforts can provide useful insights into system behavior even when data and models are simplified.

Because there will always be considerable uncertainty in input parameters, model assumptions, and model structure, and because practitioners will be predicting responses to climatic conditions that are without precedent, frameworks such as this will be best suited to making relative comparisons among management alternatives rather than estimating specific future conditions (McCarthy et al., 2003; Larson et al., 2004). Despite the inherent uncertainties, a major advantage of such model-based comparisons is that they reflect a synthesis of existing empirical evidence (Rastetter, 1996). This synthesis establishes a heuristic means, at least, for exploring complex interactions that are difficult or impossible to capture through experimentation, observation, or less synthetic modeling efforts.

## Acknowledgements

We are grateful to Sue Pierson and Barb Rosenbaum for their help processing GIS data. Josh Lawler, Thorsten Wiegand, Søren Nielsen, and two anonymous reviewers provided valuable comments on draft versions. The information in this document has been funded in part by the US EPA. It has been subjected to the Agency's peer and administrative review and approved for publication. The conclusions and opinions are solely those of the authors and are not necessarily the views of the Agency. B. McRae was partially supported as a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California.

## REFERENCES

- Adamus, P.R., Baker, J.P., White, D., Santelmann, M., Haggerty, P., 2000. Terrestrial Vertebrate Species of the Willamette River Basin: Species–Habitat Relationships Matrix. Internal Report. U.S. Environmental Protection Agency, Corvallis, OR.
- Akçakaya, H.R., Radeloff, V.C., Mladenoff, D.H., He, H.S., 2004. Integrating landscape and metapopulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. *Conserv. Biol.* 18, 526–537.
- Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species–climate impact models under climate change. *Glob. Change Biol.* 11, 1504–1513.
- Arcese, P., 1989. Intrasexual competition, mating system and natal dispersal in song sparrows. *Anim. Behav.* 38, 958–979.
- Arcese, P., Smith, J.N.M., Hochachka, W.M., Rogers, C.M., Ludwig, D., 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology* 73, 805–822.
- Arcese, P., Sogge, M.K., Marr, A.B., Patten, M.A., 2002. Song sparrow (*Melospiza melodia*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 704. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Armstrong, E.A., 1955. *The Wren*. Collins, London.
- Bart, J., 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecol. Appl.* 5, 411–420.
- Battin, J., Wiley, M.W., Ruckelshaus, M.H., Palmer, R.N., Korb, E., Bartz, K.K., Imaki, H., 2007. Projected impacts of climate change on salmon habitat restoration. *Proc. Natl. Acad. Sci. U. S. A.* 104, 6720–6725.
- Berry, P.M., Dawson, T.P., Harrison, P.A., Pearson, R.G., 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Glob. Ecol. Biogeogr.* 11, 453–462.
- Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate gradients. *Ecology* 77, 2055–2074.
- Busing, R.T., Solomon, A.M., 2004. A comparison of forest survey data with forest dynamics simulators FORCLIM and ZELIG along climatic gradients in the Pacific Northwest. U.S. Geological Survey Scientific Investigations Report. 2004–5078.
- Busing, R.T., Solomon, A.M., 2005. Assessment of a model of forest dynamics under contrasting climate and disturbance regimes in the Pacific Northwest. U.S. Geological Survey Scientific Investigations Report. 2005–5242.
- Busing, R.T., Solomon, A.M., 2006. Modeling the effects of fire frequency and severity on forests in the northwestern United States. U.S. Geological Survey Scientific Investigations Report. 2006–5061.
- Busing, R.T., Solomon, A.M., McKane, R.B., Burdick, C., 2007. Forest dynamics in Oregon landscapes: evaluation and application of an individual-based model. *Ecol. Appl.* 17, 1967–1981.
- Cairns, J., 1993. Will there ever be a field of landscape toxicology? *Environ. Toxicol. Chem.* 12, 609–610.
- Carey, A.B., Hardt, M.M., Horton, S.P., Biswell, B.L., 1991. Spring bird communities in the Oregon Coast Range. In: Ruggiero, L.F., Aubry, D.B., Carey, A.B., Huff, M.H. (Tech. Cords.), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-285. pp. 123–142.
- Carey, P.D., Brown, N.J., 1994. The use of GIS to identify sites that will become suitable for a rare orchid, *Himantoglossum hircinum* L., in future changed climate. *Biodivers. Lett.* 2, 117–123.
- Conroy, M.J., Cohen, Y., James, F.C., Matsinos, Y.G., Maurer, B.A., 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecol. Appl.* 5, 17–19.
- Cramp, S., 1988. *Handbook of the Birds of Europe, the Middle East and North Africa. Tyrant Flycatchers to Thrushes*, vol. V. Oxford University Press, Oxford, U.K.
- Crick, H.Q.P., Sparks, T.H., 1999. Climate change related to egg-laying trends. *Nature* 399, 423–424.
- Dale, V.H., 1997. The relationship between land-use and climate change. *Ecol. Appl.* 7, 753–769.
- Daly, C., Smith, J.I., McKane, R., 2007. High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. *J. Appl. Meteorol. Climatol.* 46, 1565–1586.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range response to global warming. *Nature* 391, 783–786.

- DeSante, D.F., Burton, K.M., Williams, O.E., 1993. The Monitoring Avian Productivity and Survivorship (MAPS) program second annual report (1990–1991). *Bird Popul.* 1, 68–97.
- Dullinger, S., Dirnböck, T., Grabherr, G., 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *J. Ecol.* 92, 241–252.
- Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H., Stevens, E.E., 1995. Spatially explicit population models: current forms and future uses. *Ecol. Appl.* 5, 3–11.
- Ellner, S.P., Fieberg, J., Ludwig, D., Wilcox, C., 2002. Precision of population viability analysis. *Conserv. Biol.* 16, 258–261.
- Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M., Wessels, K.J., 2002. Vulnerability of South African animal taxa to climate change. *Glob. Change Biol.* 8, 679–693.
- Fielding, A.H., Haworth, P.F., 1995. Testing the generality of bird–habitat models. *Conserv. Biol.* 9, 1466–1481.
- Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledging success in field–forest ecotones. *Ecology* 59, 871–883.
- Gilpin, M.E., 1987. Spatial structure and population vulnerability. In: Soulé, M.E. (Ed.), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK, pp. 125–139.
- Grimm, V., Railsback, S.F., 2005. *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton, NJ.
- Halliburton, R., Mewaldt, L.R., 1976. Survival and mobility in a population of Pacific Coast Song Sparrows (*Melospiza melodia gouldii*). *Condor* 78, 499–504.
- Hansen, A.J., Rotella, J.J., Kraska, M.P.V., Brown, D., 1999. Dynamic habitat and population analysis: an approach to resolve the biodiversity manager's dilemma. *Ecol. Appl.* 9, 1459–1476.
- Hejl, S.J., Holmes, J.A., Kroodsma, D.E., 2002. Winter Wren (*Troglodytes troglodytes*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 623. Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Hill, J.K., Thomas, C.D., Huntley, B., 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margins. *Proc. R. Soc. Lond. B: Biol. Sci.* 266, 197–1206.
- Holt, R.D., Pacala, S.W., Smith, T.W., Liu, J., 1995. Linking contemporary vegetation models with spatially explicit animal population models. *Ecol. Appl.* 5, 20–27.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* 15, 56–61.
- Hulse, D.W., Branscomb, A., Payne, S.G., 2004. Envisioning alternatives: using citizen guidance to map future land and water use. *Ecol. Appl.* 14, 325–341.
- Hulse, D.W., Gregory, S.V., Baker, J.P., 2002. *Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change*. Oregon State University Press, Corvallis, Oregon.
- Jepsen, J.U., Topping, C.J., Odderskær, P., Andersen, P.N., 2005. Evaluating consequences of land-use strategies on wildlife populations using multiple-species predictive scenarios. *Agric. Ecosyst. Environ.* 105, 581–594.
- Johnson, A.R., 2002. Landscape ecotoxicology and assessment of risk at multiple scales. *Hum. Ecol. Risk Assess.* 8, 127–146.
- Jorgensen, S.E., 1986. *Fundamentals of Ecological Modelling*. Elsevier, Amsterdam, Netherlands.
- Larson, M.A., Thompson, F.R., Millsaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecol. Model.* 180, 103–118.
- Lawler, J.J., Schumaker, N.H., 2004. Evaluating habitat as a surrogate for population viability using a spatially explicit population model. *Environ. Monit. Assess.* 94, 85–100.
- Leslie, P.H., 1945. On the use of matrices in certain population mathematics. *Biometrika* 33, 183–212.
- Matthews, S.N., O'Connor, R.J., Iverson, L.R., Prasad, A.M., 2004. *Atlas of climate change effects in 150 bird species of the eastern United States*. Northeastern Research Station, U.S. Department of Agriculture Forest Service, Radnor, Pennsylvania.
- McCarthy, M.A., Andelman, S.J., Possingham, H.P., 2003. Reliability of relative predictions in population viability analysis. *Conserv. Biol.* 17, 982–989.
- McCarty, J.P., 2001. Ecological consequences of recent climate change. *Conserv. Biol.* 15, 320–331.
- McLachlin, R.A., 1983. Dispersion of the western winter wren (*Troglodytes troglodytes pacificus* Baird) in coastal western hemlock forest at the University of British Columbia Research Forest in south-western British Columbia. Ph.D. Thesis. Faculty of Forestry, University of British Columbia, Vancouver, B.C. xxii + 275 pp.
- Meffe, G.K., Carroll, C.R., 1994. *Principles of Conservation Biology*. Sinauer, Sunderland, MA.
- Mooij, W.M., DeAngelis, D.L., 1999. Error propagation in spatially explicit population models: a reassessment. *Conserv. Biol.* 13, 930–933.
- Mote, P.W., Parson, E.A., Hamlet, A.F., Ideker, K.G., Keeton, W.S., Lettenmaier, D.P., Mantua, N.J., Miles, E.L., Peterson, D.W., Peterson, D.L., Slaughter, R., Snover, A.K., 2003. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. *Clim. Change* 61, 45–88.
- Nice, M.M., 1937. Studies in the life history of the Song sparrow. Part I. *Trans. Linnaean Soc. N. Y.* 6, 1–329.
- Norris, K., Atkinson, P.W., Gill, J.A., 2004. Climate change and coastal waterbird populations—past declines and future impacts. *Ibis* 146, S82–S89.
- Oreskes, N., Shrader-Frechette, K.S., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth sciences. *Science* 263, 641–646.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Peterjohn, B.G., Sauer, J.R., 1993. North American Breeding Bird Survey annual summary 1990–1991. *Bird Popul.* 1, 1–15.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33, 1689–1703.
- Rastetter, E.B., 1996. Validating models of ecosystem response to global change. *Bioscience* 46, 190–198.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.
- Root, T.L., Schneider, S.H., 2002. Climate change: overview and implications for wildlife. In: Schneider, S.H., Root, T.L. (Eds.), *Wildlife Responses to Climate Change: North American Case Studies*. Island Press, Washington, DC.
- Ruckelshaus, M., Hartway, C., Kareiva, P., 1997. Assessing the data requirements of spatially explicit dispersal models. *Conserv. Biol.* 11, 1298–1306.
- Santer, B.D., Taylor, K.E., Wigley, T.M.L., Jones, P.D., Karoly, D.J., Mitchell, J.F.B., Oort, A.H., Penner, J.E., Ramaswamy, V., Schwarzkopf, M.D., Stouffer, R.J., Tett, S.F.B., 1996. A search for human influences on the thermal structure of the atmosphere. *Nature* 382, 39–46.
- Schumaker, N.H., 1998. A User's Guide to the PATCH Model. EPA/600/R-98/135. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
- Schumaker, N.H., Ernst, T., White, D., Baker, J., Haggerty, P., 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. *Ecol. Appl.* 14, 381–401.
- Sillett, T.S., Holmes, R.T., Sherry, T.W., 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288, 2040–2042.
- Smith, J.N.M., Taitt, M.J., Rogers, C.M., Arcese, P., Keller, L., Cassidy, A., Hochachka, W.M., 1996. A metapopulation

- approach to population biology of song sparrows. *Ibis* 138, 120–128.
- Sogge, M.K., van Riper, C., 1988. Breeding biology and population dynamics of the San Miguel Island song sparrow (*Melospiza melodia micronyx*). CPSU/UCD Tech. Rep. No. 26. 120 pp.
- Tews, J., Ferguson, M.A.D., Fahrig, L., 2007. Potential net effects of climate change on High Arctic Peary caribou: lessons from a spatially explicit simulation model. *Ecol. Model.* 207, 85–98.
- Tews, J., Milton, S.J., Esther, A., Jeltsch, F., 2006. Linking a population model with a landscape model: assessing the impact of land use and climate change on savanna shrub cover dynamics. *Ecol. Model.* 195, 219–228.
- Topping, C.J., Odderskær, P., 2004. Modelling the influence of temporal and spatial factors on the assessment of impacts of pesticides on skylarks. *Environ. Toxicol. Chem.* 23, 509–520.
- Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond. B: Biol. Sci.* 270, 467–473.
- Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S., McKelvey, K., 1995. Usefulness of spatially explicit population models in land management. *Ecol. Appl.* 5, 12–16.
- van Langevelde, F., 2000. Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography* 23, 614–622.
- Villard, M.A., Taylor, P.D., 1994. Tolerance to habitat fragmentation influences the colonization of new habitat by forest birds. *Oecologia* 98.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to climate change. *Nature* 416, 389–395.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid response of British butterflies to opposing forces of climate and habitat change. *Nature* 414, 65–69.
- Wiegand, T., Moloney, K.A., Naves, J., Knauer, F., 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *Am. Nat.* 154, 605–627.